Effects of BG11 and CHU nutrient media on the laboratory cultivation of *Nostoc cf. punctiforme*: implications for sustainable production of an Andean bioresource

Efectos de los medios de cultivo BG11 y CHU en el cultivo de laboratorio de *Nostoc* cf. *punctiforme*: implicaciones para la producción sostenible de un biorrecurso andino

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ABSTRACT

Nostoc cf. punctiforme, a filamentous cyanobacterium traditionally consumed in the Andean region, is valued for its high nutritional content and its potential for sustainable aquaculture. However, increasing demand for this organism has intensified the harvesting pressure on natural populations. Cultivation strategies that improve biomass production under controlled conditions may contribute to reducing this pressure and supporting conservation-oriented management. In this study, under controlled laboratory conditions we evaluated the effects of different concentrations of BG11 and CHU culture media on the growth and biomass production of *Nostoc cf. punctiforme*. Nine treatments were tested, including a control without nutrients (T0) and four concentrations of each culture medium (25%, 50%, 100% and 125%). The cultures were maintained for 35 days in both liquid and solid media, and growth performance was assessed through wet weight, dry weight and, in liquid cultures, specific growth rate. In solid medium, the highest wet biomass was observed in treatments T3 (100% BG11) and T8 (125% CHU), reaching 2.09 g and 2.87 g, respectively. In liquid medium, treatment T2 (50% BG11) showed the highest biomass production, with an average of 1.18 g and a specific growth rate of 2.77 % d^{-1}. In contrast, the control treatment exhibited the highest dry-matter fraction, suggesting differences in water content or extracellular matrix organization among treatments, rather than higher biomass productivity. Although nutrient enrichment improved growth-related variables in several treatments, it was also associated with a reduction in the occurrence of intact colonies. These results indicate that nutrient enrichment significantly influences biomass production, growth dynamics and colony stability in *Nostoc cf. punctiforme*. Therefore, the evaluated conditions provide preliminary laboratory-scale evidence for controlled cultivation, although colony integrity will need to be improved before pilot-scale production systems can be proposed.

Keywords: *Cyanobacteria, biomass production, BG11 culture medium, CHU culture medium, colony integrity, sustainable aquaculture*

RESUMEN

Nostoc cf. punctiforme, una cianobacteria filamentosa tradicionalmente consumida en la región andina, es valorada por su alto contenido nutricional y su potencial para la acuicultura sostenible. Sin embargo, la creciente demanda de este organismo ha intensificado la presión de cosecha sobre las poblaciones naturales. Las estrategias de cultivo que mejoren la producción de biomasa bajo condiciones controladas pueden contribuir a reducir esta presión y apoyar un manejo orientado a la conservación. Este estudio evaluó el efecto de diferentes concentraciones de los medios de cultivo BG11 y CHU sobre el crecimiento y la producción de biomasa de *Nostoc cf. punctiforme* bajo condiciones controladas de laboratorio. Se evaluaron nueve tratamientos, incluyendo un control sin nutrientes (T0) y cuatro concentraciones (25 %, 50 %, 100 % y 125 %) de cada medio de cultivo. Los cultivos se mantuvieron durante 35 días tanto en medios líquidos como sólidos, y el desempeño del crecimiento se evaluó mediante peso húmedo, peso seco y, en los cultivos líquidos, tasa de crecimiento específico. En medio sólido, la mayor biomasa húmeda se observó en los tratamientos T3 (100 % BG11) y T8 (125 % CHU), hasta alcanzar 2.09 g y 2.87 g, respectivamente. En medio líquido, el tratamiento T2 (50 % BG11) mostró la mayor producción de biomasa, con un promedio de 1.18 g y una tasa de crecimiento específico de 2.77 % d^{-1}. En contraste, el tratamiento control presentó los valores más altos de peso seco, lo que sugiere diferencias en el contenido de agua o en la producción de matriz extracelular entre tratamientos más que una mayor productividad de biomasa. Aunque el enriquecimiento de nutrientes mejoró variables asociadas al crecimiento en varios tratamientos, también estuvo asociado con una reducción en la ocurrencia de colonias intactas. Estos resultados

indican que el enriquecimiento de nutrientes influye significativamente en la producción de biomasa y en la dinámica de crecimiento de *Nostoc cf. punctiforme*. Por lo tanto, las condiciones evaluadas aportan evidencia preliminar a escala de laboratorio para el cultivo controlado, aunque la integridad colonial debe mejorarse antes de proponer sistemas de producción a escala piloto.

Palabras clave: *cianobacterias, producción de biomasa, medio de cultivo BG11, medio de cultivo CHU, integridad colonial, acuicultura sostenible*

Introduction

Cyanobacteria of the genus *Nostoc*, known in Peru as '*cushuro*', '*murmuta*' or '*llullusha*' (Carhuapoma *et al*., 2015), and by other local names such as '*uvas de río*' or '*cochayuyo*' (Herrera-Pérez, 2012), have been consumed traditionally in Andean regions for centuries. Due to their high protein content and nutritional value, they have been proposed as a complementary food to combat malnutrition (Chávez, 2014) and as a source of dietary fiber and hydrocolloids with industrial applications (Jurado *et al*., 2014). Morphologically, *Nostoc* forms macroscopic gelatinous colonies composed of densely aggregated filaments enclosed in a mucilaginous matrix (Sachs *et al*., 2011), a structure that is closely related to colony cohesion, hydration and adaptation to freshwater or terrestrial environments, particularly in high-altitude Andean ecosystems.

Species such as *N. commune* and *N. sphaericum* are seasonal food resources of high nutritional importance for local communities (Li and Gao, 2004; Carvajal-Cruz, 2011; Cadena *et al*., 2013). Their presence in High Andean wetlands has facilitated their long-standing use as a traditional food resource (Ponce, 2014). In Peru, *Nostoc* species including *N. commune*, *N. punctiforme* and *N. sphaericum* are distributed across several Andean departments, with greater abundance during the rainy season in shallow freshwater environments (Jurado *et al*., 2014; Ponce, 2014; Carbajal and Vicente, 2015).

Beyond their nutritional value, *Nostoc* populations play ecological roles in High Andean wetlands, contributing to nitrogen fixation and primary productivity (Potts, 2002). These wetlands are ecologically fragile systems, sensitive to hydrological changes and climate variability. However, in South America, few studies have addressed cultivation parameters, such as salinity, temperature, pH and nutrient concentration, in a systematic manner (Ponce, 2014). Most Peruvian research has focused on animal feed applications (Carhuapoma *et al*., 2015), polysaccharide characterization (Rodríguez-Carrillo, 2016), rheological properties (Carbajal and Vicente, 2015), fertilizer potential and oil production (Do Nascimento *et al*., 2015), whereas information related to culture conditions for controlled biomass production remains limited.

From a biotechnological perspective, controlled cultivation of *Nostoc* calls for the defining of culture conditions that maintain both biomass production and colony integrity. Culture medium composition is particularly relevant, because nutrient availability may influence filament growth, mucilage production, colony structure and biomass accumulation. BG11 medium is commonly used for cyanobacteria, because it provides the inorganic nitrogen, phosphorus, trace metals and micronutrients required for photosynthetic growth (Rippka *et al*., 1979), whereas CHU medium has been widely used for freshwater algae and cyanobacteria as an alternative nutrient formulation (Chu, 1942). Therefore, comparing these media at different concentrations may help identify whether *N. punctiforme* responds better to standard cyanobacterial enrichment or to lower-input formulations suitable for controlled biomass production.

Increasing global interest in alternative protein sources has intensified the search for alternative, low-impact protein sources, and stimulated research on cyanobacteria and other low-impact bioresources (Van Dijk *et al*., 2021; UNDESA, 2022). In Andean countries, *Nostoc* constitutes an accessible and culturally embedded nutritional resource. However, limited distribution records (Ocaña-Vidal *et al*., 2016) and increased harvesting in the absence of adequate regulation (INAIGEM, 2016) raise concerns with regard to long-term sustainability. A historical precedent occurred in China, where overexploitation of *Nostoc flagelliforme* led to its protection and the banning of trade in the species (Liu and Chen, 2003; Su *et al*., 2008).

In this context, the development of controlled cultivation systems represents a crucial technical step toward the reduction of dependence upon natural populations, and the supporting of greater conservation-oriented use of this resource. Sustainable aquaculture approaches promote rational resource governance, reduce extractive pressure and support environmental stewardship (FAO, 2020). However, before cultivation can be proposed as a management alternative, it is necessary to identify nutrient conditions that promote biomass production while preserving colony morphology and culture stability. Thus, the determining of optimal culture conditions constitutes a necessary step toward the development of sustainable production systems for this Andean bioresource, and the supporting of future *ex situ* cultivation protocols under controlled conditions.

Therefore, the aim of this study was to determine the optimal concentration of BG11 and CHU media in solid and liquid substrates for the cultivation *of Nostoc cf. punctiforme*, thereby contributing to the scientific foundation required for the sustainable aquaculture development of this ancestral bioresource.

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Materials and methods

Obtaining Nostoc *samples for isolation and cultivation in the laboratory*

Colonies of *Nostoc sp.*, closely related to *N. punctiforme*, were collected at Lake Ututo (09° 51′ S, 77° 29′ W) in the Peruvian department of Ancash, at an altitude of 4427 meters, in October 2018. The lake is a perennial oligotrophic body of water with a surface area of 10.2 hectares. Samples were collected from the benthic zone near the shore using a 500 µm mesh net. During the three-day sampling period, the physicochemical parameters of the water were recorded *in situ* using a multiparameter probe (YSI Pro Plus), including pH = 7.81 and dissolved oxygen = 4.58 mg L^{-1}. Between 09:00 and 12.00, the water temperature ranged from 5.17°C to 19.01°C. The collecting was conducted without restrictions on size or morphological aspects, with mostly a spherical shape and some globular and irregular shapes of between 1 mm to 50 mm observed, with both soft and hard consistencies to the touch, and protected with an external envelope that varied between light green, dark green, dark gray-brown, dark brown and light blue in color.

The colonies collected were placed in hermetic bags with lake water and transported in a thermal container at approximately 8°C to the *Laboratorio de Larvicultura Experimental*, *Universidad Científica del Sur*, in Lima. At the laboratory, the colonies were cleaned in accordance with the protocol described by Su *et al*. (2008). The cleaned colonies (Figure 1a) were maintained for four weeks in 10 L containers with bottled spring water filtered through 0.22 µm membranes without nutrient enrichment, under constant aeration and illumination (30 µmol m-2 s-1), in order to facilitate acclimatization before the experiments were begun (Renán *et al*., 2000).

In order to confirm their taxonomy identity, the *Nostoc* colonies were first grown on solid BG11 medium under constant illumination of 30 µmol m^{-2} s^{-1} and at a temperature of 18 ± 1 °C, for 20 days. Subsequently, molecular identification was performed using partial sequences of the 16S rRNA gene. Sequencing was carried out using the Sanger method at Macrogen Inc., South Korea. Partial sequences were assembled using ChromasPro v2.7 software, generating approximately 1400 base pairs, and compared with sequences available in the GenBank database of the National Center for Biotechnology Information (NCBI, USA). The closest match corresponded to *N. punctiforme*, with a 98% similarity. Because this value is below the commonly used species-level threshold for prokaryotic identification based on 16S rRNA gene similarity, the isolate was conservatively assigned as *Nostoc cf. punctiforme*, which is closely related to *N. punctiforme* (Kim *et al*., 2014).

Culture in solid medium (agar)

For solid medium culture, four concentrations of BG11 medium (Rippka *et al*., 1979) four concentrations of CHU medium (Chu, 1942) and a control treatment without nutrient enrichment were evaluated. The concentrations used for both BG11 and CHU media were defined according to the amount recommended for cyanobacteria by the product specifications, previous assays and references from Cadena *et al*. (2013) and Ortiz-Moreno *et al*. (2020) (Table 1). Each treatment was prepared with agar at a final concentration of 1.80% using distilled water and the corresponding BG11 and CHU concentration. After preparation and sterilization, the medium was allowed to cool before the incorporation of 100 µg of cyanocobalamin, and then distributed into sterile Petri plates for solidification and storage.

Table 1. Treatments used for the cultivation of *Nostoc cf. punctiforme* in solid and liquid media. The treatments included four relative concentrations of BG11 medium (T1-T4), four relative concentrations of CHU medium (T5-T8), and a non-enriched control treatment (T0).

Treatment	Culture medium	Concentration (g L^{-1})	Relative concentration of the full medium formulation* (%)
T0	Control	0	0
T1	BG11	0.4	25
T2	BG11	0.8	50
T3	BG11	1.6	100
T4	BG11	2.0	125
T5	CHU	0.03	25
T6	CHU	0.06	50
T7	CHU	0.12	100
T8	CHU	0.15	125

Note. *Relative concentrations were calculated based on the recommended full-strength concentration of each culture medium used in this study. Because BG11 and CHU differ in their absolute composition and concentration, the treatments were compared using the relative percentage of each full medium formulation. The concentrations were selected based on product recommendations, previous assays and the criteria reported by Cadena *et al*. (2013) and Ortiz-Moreno *et al*. (2020).

For the initial inoculation, the colonies were disinfected with 75% alcohol, in order to reduce the presence of external cells attached to the colony envelope. To verify the purity of the *Nostoc* inoculum, a drop of mucilage was extracted using a sterilized syringe and observed microscopically. Inoculation was performed in a biosafety cabinet (Telstar® Bio Advance 2) using 0.2 mL of homogenized mucilage suspension spread on each plate with a Drigalski spatula. The inoculum was standardized by homogenizing the extracted mucilage before plating and by applying the same volume to each replicate plate. However, filament density was not quantified before inoculation; therefore, the biomass results in solid medium were interpreted as final production responses, rather than as true growth rates. Finally, the inoculated plates were incubated in a germination chamber (Tecnal LED TE-

4020) at 18 ± 1 °C and constant lighting (30 µmol m^{-2} s^{-1}). Each treatment was established in independent replicate plates and randomly distributed within the incubation chamber, in order to reduce potential positional effects, such as microgradients of temperature or irradiance. No medium replacement was performed in solid agar cultures during the 35-day incubation period.

Culture in liquid medium

Liquid cultures were carried out in 250 mL flasks containing 200 mL of culture medium (Figure 1b). Bottled spring water was used and enriched with four concentrations of BG11 and CHU medium, in addition to a control treatment without enriched medium. The same proportions and dilutions used in solid medium were applied to all liquid treatments (Table 1). Each culture started with ten colonies with an average initial wet weight of 0.57 ± 0.07 g per replicate, and four replicates were established for each treatment. The experiment was conducted under constant light intensity (30 µmol m^{-2} s^{-1}), an average temperature of 19.5 ± 0.76 °C, pH of 8.66 ± 0.35 and constant aeration, for 35 days.

In liquid cultures, the culture medium was completely replaced weekly. This replacement was performed only in liquid cultures and not in solid agar cultures. During each weekly evaluation, discarded culture medium was removed, following the recommendations of Diao and Yang (2014). Wet weight (g) and total length (mm) were measured weekly only in liquid cultures, using an analytical balance (ADAM SAB 12I) and a digital Vernier (Ubermann 150), respectively. Together with these evaluations, physicochemical variables of the culture medium, including temperature (°C), pH, dissolved oxygen (mg L^{-1}), were recorded using a multiparameter probe (YSI Pro Plus). At the end of the experiment, colonies from both solid and liquid treatments were harvested, and samples were dried at 65 °C for 72 hours to determine dry biomass (Chili-Rodríguez and Terrazas-Viza, 2010). In solid cultures, only final wet and dry biomass were determined, because repeated non-destructive measurements of biomass and colony length were not feasible in agar plates.

Growth rate

The specific growth rate (SGR) was calculated using wet weight data recorded from the beginning to the end of the experiment. SGR was calculated only for liquid cultures, considering the total weight of colonies in each replicate of BG11, CHU and control treatments over the 35-day experimental period. The SGR was calculated using the following equation:

$$SGR\ (\%d^{-1} = \frac{[\ln(WF) - \ln(WI)]}{t}\ (100)$$

where WF is the final wet weight, WI is the initial wet weight, and t is the time interval between both observations, expressed in days (Fernández-Méndez *et al*., 2019). SGR was not calculated for solid cultures, because the inoculum was applied as a standardized mucilage volume, rather than as individually weighed colonies, and repeated biomass measurements during incubation were not possible without disturbing the agar cultures.

Occurrence of colonies

In liquid medium cultures, the occurrence of intact colonies was recorded weekly. Partially open or fully disintegrated colonies, defined as colonies with an open mucilaginous envelope, loss of cohesive structure, or fragmentation into dispersed filaments with no recognizable colonial form, were recorded and removed from the flasks. Accordingly, occurrence was expressed as the number of intact colonies remaining per flask at each weekly observation. This variable was evaluated only in liquid cultures, where individual colonies could be followed over time.

Statistical analysis

The data obtained were analyzed using RStudio 1.3.959 software, with a significance level of 0.05. Differences in the growth variables of *Nostoc cf. punctiforme* among the nine treatments (T0-T8) were evaluated separately for solid and liquid cultures. Because BG11 and CHU differ in their absolute concentrations (g L^{-1}), nutrient levels were primarily interpreted as percentages of the full medium formulation (0-125%), in order to facilitate comparisons between media.

Prior to selecting the statistical approach, normality and homoscedasticity were evaluated using the Jarque-Bera and Bartlett tests, respectively. Because the assumptions required for parametric analysis were not consistently met across all response variables, non-parametric methods were applied where appropriate. Dry weight in liquid cultures was the only response variable that met parametric assumptions; therefore, a two-way ANOVA was applied considering culture medium (BG11, CHU, and control) and nutrient level (expressed as a % of the full formulation) as fixed factors, followed by Tukey *post hoc* comparisons.

Conversely, for wet weight, total length, specific growth rate (SGR), colony occurrence in liquid culture, and wet and dry weights in solid culture, the data did not meet parametric assumptions. Therefore, a non-parametric approach was applied using the Scheirer-Ray-Hare (SRH) test, in order to evaluate the effects of culture medium and nutrient level. When significant differences among treatments were detected, pairwise comparisons were performed using Dunn's *post hoc* test with Bonferroni correction.

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Results

Culture in solid medium (agar)

In solid cultures, *Nostoc cf. punctiforme* showed clear differences in growth pattern depending on the culture medium. In CHU medium, the cultures did not form typical colonies composed of numerous filaments enclosed in a gelatinous matrix; instead, they showed predominantly free filaments, embedded in a transparent mucilaginous structure (Figure 1c-1d). In contrast, those cultures grown in BG11 medium developed visible envelopes and circular colony-like structures (Figure 1e-1f).

Final wet biomass in solid medium was numerically lowest in the control treatment T0 (0.045 ± 0.07 g). Most nutrient-enriched treatments showed higher final wet biomass than the control, although statistical separation was clearest for the treatments with the highest biomass values. In BG11 medium, the highest wet biomass was recorded in T3 (100% BG11; 2.087 ± 1.42 g), followed by T2 (50% BG11; 1.226 ± 0.59 g), whereas T4 (125% BG11; 0.675 ± 0.28 g) showed a lower value than T3. In CHU medium, wet biomass increased toward the highest concentration, with T8 (125% CHU; 2.873 ± 1.48 g) showing the highest value, followed by T7 (100% CHU; 1.611 ± 1.30 g). According to the *post hoc* comparisons, T3 and T8 were included in the highest statistical group, whereas T0 was included in the lowest group (Table 2).

A similar pattern was observed for dry biomass in solid medium. The lowest dry weight was recorded in T0 (0.009 ± 0.01 g), whereas the highest values were observed in T3 (0.077 ± 0.07 g) and T8 (0.056 ± 0.03 g). Overall, the highest final biomass values in solid medium were associated with 100% BG11 and 125% CHU.

Culture in liquid medium

Wet weight

In liquid cultures, wet biomass increased over time in most enriched treatments (Figure 2). The highest final wet weight was recorded in T2 (50% BG11; 1.178 ± 0.33 g), followed by T6 (50% CHU; 1.0595 ± 0.44 g), T8 (125% CHU; 1.0222 ± 0.54 g) and T5 (25% CHU; 1.0152 ± 0.38 g). The lowest final wet weights were observed in T4 (125% BG11; 0.7619 ± 0.14 g) and T0 (0.7766 ± 0.17 g). During the temporal evaluation, T2 reached the highest wet biomass on Day 28 (1.2917 ± 0.45 g), followed by a slight decrease by Day 35 (Figure 2). According to the *post hoc* comparisons, T2 was included in the highest statistical group and differed from the lowest-biomass treatments T0 and T4, whereas the remaining enriched treatments showed intermediate values and shared statistical letters with at least one of those groups (Table 2).

Total length

Total length followed a similar trend to wet biomass in liquid cultures. The highest final values were recorded in T2 (50% BG11; 13.26 ± 1.33 mm) and T6 (50% CHU; 12.70 ± 1.45 mm), whereas the lowest values were observed in T4 (125% BG11; 11.53 ± 0.62 mm) and T0 (11.60 ± 0.63 mm) (Figure 2, Table 2). *Post hoc* comparisons showed that T2 was included in the highest statistical group, while T0 and T4 were included in the lowest group; the remaining treatments showed intermediate responses. These results indicate that low to intermediate nutrient concentrations, particularly 50% BG11 and 50% CHU, favored greater colony size in liquid medium, while the absence of enrichment or the highest BG11 concentration was associated with smaller colonies. As observed for wet biomass, maximum colony length tended to occur before the end of the experimental period, particularly around Day 28 in the best-performing treatments (Figure 2).

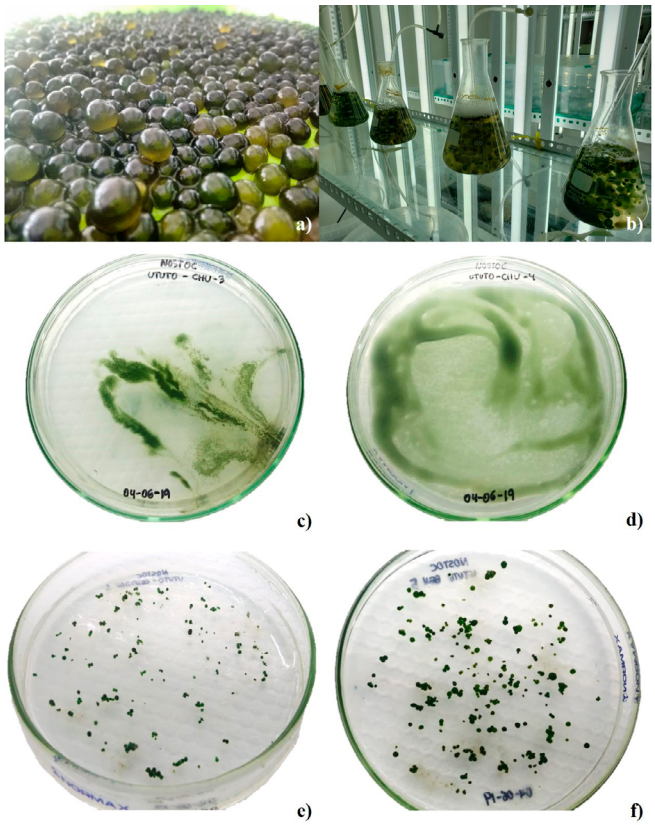

Figure 1. Growth evaluation of *Nostoc cf. punctiforme* under different culture conditions. a) Colonies collected from Lake Ututo; b) liquid culture system in flasks with constant illumination and aeration; c-d) appearance of cultures grown in CHU solid medium, showing predominantly filamentous growth within a mucilaginous matrix; e-f) appearance of cultures grown in BG11 solid medium, showing more defined colony-like structures. All culture systems are shown after 35 days of cultivation.

Table 2. Mean ± standard deviation of wet and dry biomass in solid medium, and wet biomass, dry biomass, total length, and specific growth rate in liquid medium, for four treatments enriched with BG11 medium (T1-T4), four treatments enriched with CHU medium (T5-T8) and a control treatment without nutrient enrichment (T0) after 35 days of *Nostoc cf. punctiforme* cultivation.

Treatment	Culture medium	Solid medium		Liquid medium			
		Wet weight (g)*	Dry weight (g)*	Wet weight (g)*	Dry weight (g)**	Total length (mm)*	Specific growth rate (% d^{-1}) *
T0	Control	0.045 ± 0.07^{c}	0.009 ± 0.01^{c}	0.7766 ± 0.17^{b}	0.2419 ± 0.03^{a}	11.60 ± 0.62^{b}	0.8155 ± 0.04^{c}
T1	BG11	0.231 ± 0.2^{bc}	0.016 ± 0.01^{bc}	0.9799 ± 0.38^{ab}	0.1720 ± 0.06^{b}	12.59 ± 1.30^{ab}	2.7022 ± 0.11^{a}
T2	BG11	1.226 ± 0.59^{ab}	0.026 ± 0.004^{abc}	1.178 ± 0.33^{a}	0.2324 ± 0.03^{ab}	13.26 ± 1.30^{a}	2.7733 ± 0.09^{a}
T3	BG11	2.087 ± 1.42^{a}	0.077 ± 0.07^{a}	0.9427 ± 0.20^{ab}	0.1877 ± 0.05^{b}	12.58 ± 0.92^{ab}	1.8454 ± 0.10^{abc}
T4	BG11	0.675 ± 0.28^{abc}	0.019 ± 0.004^{bc}	0.7619 ± 0.14^{b}	0.1603 ± 0.01^{b}	11.53 ± 0.61^{b}	0.9925 ± 0.05^{bc}
T5	CHU	0.613 ± 0.38^{abc}	0.016 ± 0.01^{bc}	1.0152 ± 0.38^{ab}	0.1763 ± 0.01^{b}	12.42 ± 1.36^{ab}	2.3244 ± 0.04^{abc}
T6	CHU	0.698 ± 0.54^{abc}	0.020 ± 0.02^{bc}	1.0595 ± 0.44^{ab}	0.2000 ± 0.04^{ab}	12.70 ± 1.42^{ab}	2.4752 ± 0.09^{ab}
T7	CHU	1.611 ± 1.30^{ab}	0.038 ± 0.02^{ab}	0.9987 ± 0.38^{ab}	0.1512 ± 0.06^{b}	12.30 ± 1.40^{ab}	1.8172 ± 0.11^{abc}
T8	CHU	2.873 ± 1.48^{a}	0.056 ± 0.03^{a}	1.0222 ± 0.54^{ab}	0.1707 ± 0.04^{b}	12.29 ± 1.61^{ab}	2.2347 ± 0.10^{abc}

Notes. * Different superscript letters within the same column indicate significant differences among treatments ($p < 0.05$), according to Dunn's *post hoc* test with Bonferroni correction. Treatments sharing at least one letter are not significantly different.
** Different superscript letters within the same column indicate significant differences among treatments ($p < 0.05$), according to Tukey's *post hoc* test after two-way ANOVA. Treatments sharing at least one letter are not significantly different.

Dry weight

Significant differences were observed in dry biomass among treatments in liquid cultures. The control treatment T0 showed the highest average dry weight (0.2419 ± 0.03 g), followed by T2 (50% BG11; 0.2324 ± 0.03 g) and T6 (50% CHU; 0.2000 ± 0.04 g). In contrast, the lowest values were recorded in T7 (100% CHU; 0.1512 ± 0.06 g), T4 (125% BG11; 0.1603 ± 0.01 g) and T8 (125% CHU; 0.1707 ± 0.04 g) (Table 2). According to Tukey's *post hoc* comparisons, T0 was included in the highest statistical group, while T2 and T6 showed intermediate values that shared letters with the highest group.

Although T0 had one of the lowest wet weights, it presented the highest dry-matter fraction, equivalent to approximately 31% of its wet biomass. In enriched treatments, the dry-matter fraction was lower, generally ranging between approximately 15% and 21%. Therefore, dry weight and wet weight showed different response patterns among treatments. This pattern is further addressed in the discussion section.

Specific growth rate (SGR)

The specific growth rate (SGR) was calculated only for liquid cultures. The highest SGR values were recorded in T2 (50% BG11; 2.7733 ± 0.09% d^{-1}), T1 (25% BG11; 2.7022 ± 0.11% d^{-1}) and T6 (50% CHU; 2.4752 ± 0.09% d^{-1}). The control treatment T0 showed the lowest SGR (0.8155 ± 0.04% d^{-1}), followed by T4 (125% BG11; 0.9925 ± 0.05% d^{-1}) (Table 2). *Post hoc* comparisons indicated that T1 and T2 were included in the highest statistical group, whereas T0 was included in the lowest group. T4 showed a low to intermediate response, while the remaining enriched treatments showed intermediate SGR values. These results show that nutrient enrichment increased SGR in liquid medium, particularly at low to intermediate concentrations, whereas the highest BG11 concentration did not improve growth rate.

SGR was not calculated for solid cultures because the initial inoculum was applied as a homogenized mucilage volume, rather than as individually weighed colonies, and repeated biomass measurements during incubation were not feasible without disturbing the agar cultures.

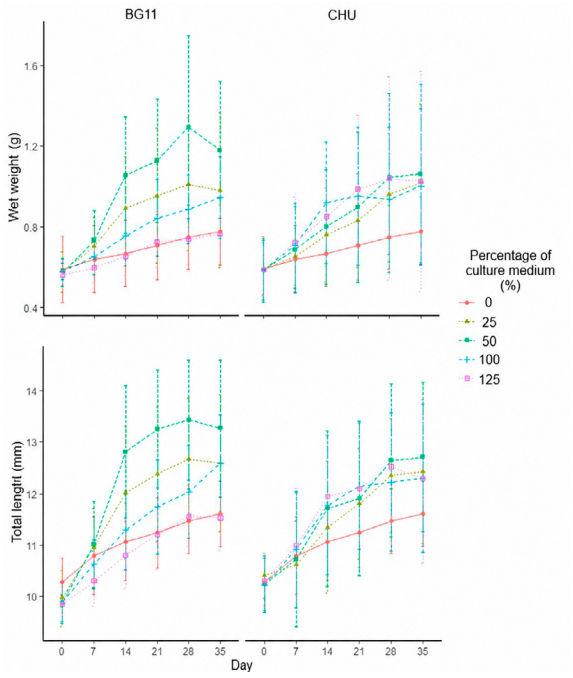

Figure 2. Average wet weight (g) and total length (mm) of *Nostoc cf. punctiforme* colonies grown in liquid medium using different percentages of CHU and BG11 media, over 35 days.

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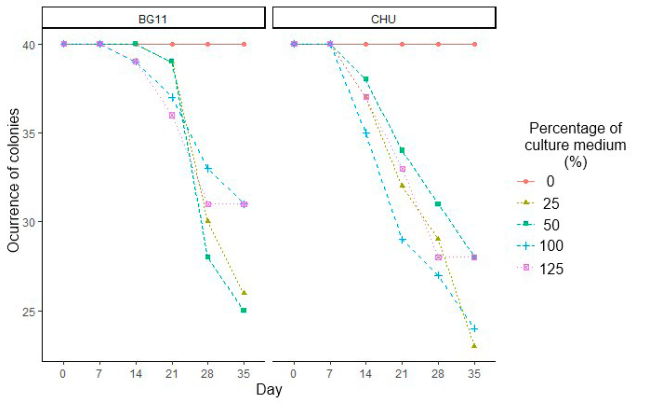

Figure 3. Occurrence of intact colonies of *Nostoc cf. punctiforme* grown in liquid medium using different percentages of CHU and BG11 media, over 35 days.

Occurrence of colonies

In liquid medium cultures, colony occurrence decreased over time in all nutrient-enriched treatments, whereas the control treatment T0 maintained the initial number of colonies until the end of the experiment (Figure 3). The greatest reductions were observed in CHU treatments, particularly T5 and T7, while BG11 treatments also showed a progressive reduction in intact colonies after the first weeks of culture. This pattern indicates that nutrient enrichment promoted biomass increase in several treatments but was also associated with a reduction in the number of intact colonies maintained over time.

Overall interpretation of results

Overall, the results show that nutrient enrichment modified wet biomass, colony size, and SGR in liquid cultures, with the best responses generally observed at low to intermediate concentrations, such as 50% BG11 and 50% CHU. In solid medium, the highest final biomass values were observed in 100% BG11 and 125% CHU. However, the higher dry-matter fraction observed in the control and the reduction of colony occurrence in enriched liquid treatments indicate that biomass production and colonial integrity responded differently to nutrient enrichment.

Discussion

Cultivation responses under controlled conditions

In our study, *Nostoc cf. punctiforme* was successfully maintained under controlled laboratory conditions using BG11 and CHU media at different nutrient concentrations. The results demonstrate that nutrient enrichment significantly affected biomass production, colony morphology, growth rate and colony integrity. Biomass production was maximized under intermediate nutrient concentrations in liquid culture and under higher nutrient concentrations in solid culture. However, enhanced biomass production was accompanied by a reduction in the occurrence of intact colonies, indicating a trade-off between growth performance and colony stability. Therefore, the suitability of a culture medium for *Nostoc* cultivation should be evaluated not only according to biomass yield, but also considering the preservation of colony structure, which constitutes a critical attribute for future scaling and sustainable production systems (De Philippis *et al*., 2000; Borowitzka, 2013).

Cyanobacteria of the genus *Nostoc* are naturally adapted to low-temperature and nutrient-limited environments, including High Andean ecosystems (Potts, 2002). In this study, *Nostoc cf. punctiforme* was maintained under controlled laboratory conditions, with temperature and pH values within ranges previously reported as suitable for the growth of other *Nostoc* species (López-López and Serna-Hernández, 1999; Moncayo, 2017). These results indicate that the strain can remain viable under laboratory cultivation; however, the response differed depending on culture medium, nutrient concentration and culture system.

In solid cultures, BG11 promoted the formation of more defined colony-like structures with visible envelopes, whereas CHU favored predominantly filamentous growth within a mucilaginous matrix. This difference suggests that nutrient composition influenced not only biomass accumulation but also colonial morphology. The development of structured colonies in BG11 is consistent with the importance of exocellular investments in *Nostoc* strains (De Philippis *et al*., 2000). In contrast, the filamentous and less organized growth observed in CHU indicates that this medium may favor cellular expansion without maintaining the same degree of colonial organization. Therefore, the choice of medium should not be based only on final biomass, but also on the type of growth obtained.

In liquid cultures, low to intermediate nutrient concentrations produced the best growth responses. Treatment T2 (50% BG11) showed the highest wet biomass and SGR, while T6 (50% CHU) also showed favorable values for colony length and growth. This pattern suggests that moderate nutrient enrichment was sufficient to promote biomass increase, whereas higher nutrient concentration did not necessarily improve growth. In particular, the lower response observed in T4 (125% BG11) indicates that nutrient excess may limit performance in liquid culture. Similar responses have been reported in cyanobacteria and microalgae, where nutrient availability can stimulate growth up to an optimum level, but unbalanced or excessive enrichment may alter physiological performance and biomass quality (Borowitzka, 2013; Chen *et al*., 2021).

The contrasting pattern observed between wet weight and dry weight calls for cautious interpretation. Although the control treatment showed the highest dry-matter fraction, it also showed one of the lowest wet biomass values and the lowest SGR. Therefore, the higher dry weight

observed in T0 should not be interpreted as evidence of superior biomass productivity. Rather, it indicates that colonies grown without nutrient enrichment had a higher proportion of dry matter relative to hydrated biomass. Wet weight remains relevant because *Nostoc* colonies are naturally hydrated and are commonly handled as fresh biomass; however, dry weight provides a more conservative indicator of structural biomass. For this reason, both variables should be interpreted together.

The higher dry-matter fraction in T0 may be related to differences in colony hydration, mucilage retention or extracellular matrix organization. However, this interpretation should be considered hypothetical, given that the carbohydrate/protein ratios, EPS yield and biochemical composition of the extracellular matrix were not measured in this study. Previous studies have shown that *Nostoc* strains can produce complex exocellular polysaccharide structures and that the composition of these matrices may vary among strains and culture conditions (De Philippis *et al.*, 2000; Jensen *et al.*, 2013; Laroche, 2022). Accordingly, future studies should include biochemical characterization of the extracellular matrix, in order to determine whether changes in dry-matter fraction are associated with EPS production, protein content, or with other structural components. Therefore, the interpretation of dry weight as an indicator of biological productivity should be made cautiously in *Nostoc* colonies, because changes in hydration state and extracellular matrix composition may substantially influence biomass measurements (De Philippis *et al.*, 2000; Jensen *et al.*, 2013).

Colony integrity as a limiting factor

A central finding of this study was the reduction in the occurrence of intact colonies in nutrient-enriched treatments. Although several enriched treatments showed higher biomass production and growth rates than the control, they also exhibited a greater loss of colony integrity over time. In contrast, colonies maintained in the control treatment remained structurally stable throughout the experimental period. This pattern suggests that nutrient availability may influence not only growth but also the organization and maintenance of the mucilaginous matrix that characterizes *Nostoc* colonies (De Philippis *et al.*, 2000; Pereira *et al.*, 2005).

The mechanisms responsible for colony disintegration were not directly evaluated in this study; however, previous studies have reported that changes in nutrient availability can modify extracellular polysaccharide production, filament aggregation and colony cohesion in cyanobacteria (De Philippis *et al.*, 2000; Jensen *et al.*, 2013; Corrales *et al.*, 2017). Under nutrient-rich conditions, accelerated cellular proliferation may occur without proportional reinforcement of the extracellular matrix, potentially increasing the susceptibility of colonies to fragmentation. Also, elevated concentrations of dissolved salts and nitrogen compounds may alter the physicochemical properties of the mucilage and affect colony cohesion. These interpretations should be considered as hypotheses requiring experimental confirmation through analyses of extracellular polymeric substances (EPS), osmotic regulation and colony ultrastructure (Aboal *et al.*, 2020; Corrales *et al.*, 2017).

From an applied perspective, colony integrity appears to be a critical criterion for evaluating cultivation success. While treatments such as T2 and T6 promoted superior growth performance, the simultaneous reduction in intact colonies indicates that biomass productivity alone may not adequately reflect culture quality. Future optimization strategies should therefore aim to maximize biomass production while maintaining colony stability, since both attributes are necessary for the development of reliable cultivation protocols and future scale-up applications (De Philippis *et al.*, 2000; Jensen *et al.*, 2013).

Implications for sustainable cultivation and conservation-oriented use

The results of this study provide laboratory-scale evidence that controlled cultivation of *Nostoc cf. punctiforme* is feasible and that nutrient concentration strongly affects biomass production and morphology. However, the present study does not directly quantify harvesting pressure, regeneration rates or population dynamics in natural High Andean wetlands. Therefore, conservation implications should be treated as potential applications of the cultivation results, rather than as measured ecological outcomes.

This distinction is important because the High Andean lakes of South America are ecologically sensitive systems, where *Nostoc* populations contribute to nutrient cycling and primary productivity (Potts, 2002; Do Nascimento *et al.*, 2015). Increasing demand, limited distribution records and insufficient monitoring have led to concerns about the sustainability of wild harvesting (INAIGEM, 2016; Ocaña-Vidal *et al.*, 2016). The case of *Nostoc flagelliforme* in China, where overexploitation led to protection and trade restrictions, illustrates the importance of developing preventive management strategies before depletion occurs (Liu and Chen, 2003; Su *et al.*, 2008).

In this context, *ex situ* cultivation should be viewed as one component of a broader sustainability strategy, not as an immediate replacement for ecological management. Controlled production has the potential to reduce dependence on natural populations, but only if cultivation protocols achieve stable biomass production, maintain colony integrity and are integrated with the monitoring of natural banks. Thus, the main contributions of the present study are the identifying of nutrient conditions that improve growth under laboratory conditions, and how colony disintegration constitutes a critical bottleneck for future scale-up.

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Future research will need to focus on pilot-scale validation under greenhouse or outdoor conditions, while evaluating productivity, nutrient-use efficiency, operational costs, biochemical composition and colony stability (Borowitzka, 2013; Rosales-Loaiza *et al*., 2017; FAO, 2020; Chen *et al*., 2021; Vijayaram *et al*., 2024). At the same time, cultivation studies should be coupled with ecological monitoring of natural populations, in order to determine whether cultured biomass can effectively reduce harvesting pressure.

Conclusions

This study presents laboratory-scale evidence of the response of *Nostoc cf. punctiforme* to different concentrations of BG11 and CHU media, thereby contributing to the development of controlled cultivation protocols for this ancestral Andean cyanobacterium. Among the evaluated treatments, BG11 medium exhibited greater suitability for structured colony formation, particularly at 50% concentration in liquid cultures and 100% in solid cultures, where higher biomass production and more defined colonial morphology were observed. In contrast, CHU medium promoted predominantly filamentous growth, suggesting that nutrient composition influences both biomass accumulation and colony architecture.

These results indicate that moderate nutrient enrichment can improve wet biomass, colony size and specific growth rate under controlled liquid culture conditions, particularly at low to intermediate concentrations, with the best responses observed mainly under 50% BG11 and 50% CHU. However, the higher dry-matter fraction observed in the control treatment and the reduction in the occurrence of intact colonies in enriched liquid treatments demonstrate that biomass production and colonial integrity responded differently to nutrient enrichment. Thus, increased growth did not necessarily correspond to greater culture stability.

Therefore, although the evaluated conditions provide useful information for controlled biomass production, colony integrity remains a critical limiting factor that must be resolved before pilot-scale or commercial cultivation systems can be proposed. Future studies will need to optimize nutrient concentration, harvest timing, renewal frequency, extracellular matrix stability, biochemical composition of the extracellular matrix, and long-term culture performance, in order to improve both productivity and colony stability.

Although this study did not directly evaluate harvesting pressure or population dynamics in natural populations, the cultivation responses identified here provide a preliminary technical basis for future ex situ production strategies. Such strategies have the potential to contribute to a reduction in dependence upon wild harvesting, but only if they are integrated with the ecological monitoring and sustainable management of natural High Andean populations.

Overall, the findings of this study support the controlled cultivation of *Nostoc cf. punctiforme* as a promising but still developing approach to the sustainable use of this culturally important Andean bioresource, while emphasizing that further optimization is required before its application at pilot or commercial scale can be proposed.

Authors' contributions

EDEL: Investigation, methodology, statistical analysis, writing (original draft), writing (review and editing).

PMBG: Conceptualization, methodology, investigation, writing (review and editing), visualization, supervision, project administration.

GMÁB: Fieldwork, laboratory support, investigation, writing (review and editing).

MSCF: Conceptualization, data curation, writing (original draft), writing (review and editing).

ATA: Conceptualization, investigation, statistical analysis, writing (review and editing).

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Conflicts of interest

The authors declare that they have no conflicts of interest.

Artificial Intelligence disclosure

The authors declare that no generative artificial intelligence tools were used in the design, experimentation, data generation, analysis or interpretation of this study. Artificial intelligence (generative AI tools for language editing) was used solely for language editing and improving clarity and readability. All scientific content, data interpretation and conclusions were produced in their entirety by the authors.

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